

OPINION

Canopy duration has little influence on annual carbon storage in the deciduous broad leaf forest

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Abstract

Vegetation phenology, the study of the timing and length of the terrestrial growing season and its connection to climate, is increasingly important in integrated Earth system science. Phenological variability is an excellent barometer of short- and long-term climatic variability, strongly influences surface meteorology, and may influence the carbon cycle. Here, using the 1895–1993 Vegetation/Ecosystem Modelling and Analysis dataset and the Biome-BGC terrestrial ecosystem model, we investigated the relationship between phenological metrics and annual net ecosystem exchange (NEE) of carbon. For the 1167 deciduous broad leaf forest pixels, we found that NEE was extremely weakly related to canopy duration (days from leaf appearance to complete leaf fall). Longer canopy duration, did, however, sequester more carbon if warm season precipitation was above average. Carbon uptake period (number of days with net CO₂ uptake from the atmosphere), which integrates the influence of all ecosystem states and processes, was strongly related to NEE. Results from the Harvard Forest eddy-covariance site supported our findings. Such dramatically different results from two definitions of 'growing season length' highlight the potential for confusion among the many disciplines engaged in phenological research.

Keywords: Biome-BGC, carbon cycle, growing season, net ecosystem exchange, phenology

Received 25 January 2002; revised version received and accepted 24 May 2002

Introduction

Vegetation phenology, the study of the timing and length of the terrestrial growing season and its connection to climate, has evolved from a naturalistic field into a significant Earth system science (Penuelas & Filella, 2001). For example, researchers have shown: (1) ground based data often indicating, in spite of some potential errors (Sagarin, 2001), a trend toward earlier spring growth (Schwartz & Reiter, 2000; Menzel *et al.*, 2001), (2) remotely sensed evidence of an expanded growth period (Zhou *et al.*, 2001) and responsiveness to El Niño events (Asner *et al.*, 2000), and (3) a phenological influence on surface meteorology (Durre & Wallace, 2000; Fitzjarrald *et al.*, 2001).

Plant phenology also may affect the terrestrial carbon cycle. Phenological variation, for instance, helps account for trends in the amplitude and timing of the atmospheric CO₂ cycle (Keeling *et al.*, 1996; Randerson *et al.*, 1999), seasonal variation in eddy-covariance measured fluxes (Baldocchi *et al.*, 2001), and annual net ecosystem exchange (NEE) variability (Schimel, 2001); where NEE = gross primary production (GPP) – autotrophic respiration (Ra) – heterotrophic respiration (Rh) – disturbance fluxes. Modelling studies have shown that failure to regulate phenology may induce extensive errors in simulated NEE (White *et al.*, 1999a). Several efforts have therefore either explored the need for phenology models (Schwalm & Ek, 2001) or attempted to develop prognostic phenology schemes (White *et al.*, 1997; Botta *et al.*, 2000).

In spite of these efforts, the connection between phenological variability and the terrestrial carbon cycle is incompletely understood. Consider that even for the deciduous broad leaf forest (DBF), a particularly

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well-studied biome, at least four categories of phenological metrics exist: (1) meteorological approaches such as frost-free duration, (2) visual measurements of foliage appearance and senescence, (3) remotely sensed estimates of the initiation and completion of growth (Chen *et al.*, 2000; White *et al.*, 2002), and (4) ecophysiological approaches such as the carbon uptake period (number of days with net CO₂ uptake from the atmosphere). This multiplicity of phenology definitions, all of which could be used to define growing season length (GSL) has led to considerable confusion. Findings that one measure of GSL length is related to NEE, for example, should not be interpreted to mean that GSL by any definition is related to NEE.

Our overall goal in this research was, for the eastern United States DBF, to test the null hypothesis that inter-annual phenological variation (measured with two approaches) and NEE are unrelated. Secondly, we investigated potential interactions among phenology, precipitation, and NEE. To do so we conducted simulations of twentieth century phenological variation and NEE using the Biome-BGC model and the Vegetation/Ecosystem Modelling and Analysis Project (VEMAP) dataset.

Materials and methods

Model description

We used the prognostic Biome-BGC terrestrial ecosystem model to simulate daily fluxes and states of carbon, water, and nitrogen. Model theory, including recent updates to belowground processes, a comparison with eddy-covariance data, and model parameterization are available elsewhere (White *et al.*, 2000; Thornton *et al.*, 2002). Conceptually, higher temperatures will lead to longer growing seasons (see below) and higher photosynthetic potential due to increased enzyme activation. However, higher temperatures are also associated with exponential increases in *R_a* and *R_h*. Thus warm conditions accompanied by drought-induced reduction in stomatal gas exchange can lead to reduced net carbon uptake or even net carbon release. In these conditions, higher temperatures and longer growing season may not be beneficial for carbon storage (Nemani *et al.*, 2002).

The meteorology-driven phenology subroutine used in Biome-BGC to determine canopy duration, developed from satellite-derived phenological observations (White *et al.*, 1997), is based on a climatically controlled thermal summation such that warm sites require a larger thermal summation in order to initiate growth than do cold sites. Fall senescence is photoperiod-controlled but may be advanced by cold temperatures or prolonged by warm temperatures. Canopy duration is dominantly controlled

by temperature such that warm springs will advance the timing of growth and cool springs will delay growth; variation in fall phenology is comparatively minor. The phenology model was shown to relate well to measured inter-annual variability in a ground-based phenology observation network (White *et al.*, 1997) and to independent climatic signals (Keyser *et al.*, 2000). The satellite phenology signal which the model is designed to predict corresponds to the initial stages of leaf expansion by dominant overstory species (White *et al.*, 1999b). Note that canopy duration is not interchangeable with other definitions of GSL, such as the duration of stem increment, and refers only to the number of days with a vegetation canopy present.

Simulations and analysis

We used the 0.5° × 0.5° VEMAP dataset (Schimel *et al.*, 2000) for (1) daily meteorological records of temperature, precipitation, shortwave radiation, and vapour pressure deficit, (2) soil depth and texture, and (3) land cover. We conducted Biome-BGC simulations for the 1167 VEMAP pixels containing the DBF land cover class; we used the preindustrial VEMAP meteorological record for the spinup process and the historical (1895–1993) meteorological record for analysis. To avoid confounding the effects of phenological variability with the effects of industrialization, we used constant preindustrial conditions of atmospheric CO₂ and nitrogen deposition as described in (White *et al.*, 2000). Our simulations thus represent non-industrial, equilibrium conditions.

For every pixel, we calculated annual phenological variation with two approaches: (1) ecophysiological, using the carbon uptake period, and (2) physical, using canopy duration (the number of days from leaf appearance to full leaf fall, see description above). Other metrics of physical phenology, including days from first leaf appearance to maximum leaf area index (LAI), date of half-maximum LAI, and date of maximum LAI, showed similar patterns to canopy duration and are not presented. Additionally, we calculated total warm season precipitation (April 1 – September 30). We next calculated the coefficient of determination, slope, and significance of the relationship between the phenological metrics and NEE. We then assessed lags in the relationships. To test for interactions with precipitation, we calculated each pixel's average canopy duration and warm season precipitation and identified each year as having above- or below-average canopy duration and warm season precipitation. From these classifications, we created the following four scenarios: long and wet (LW); long and dry (LD); short and wet (SW); and short and dry (SD). LW, for example, would be all years for a given pixel with above-average canopy duration and

above-average warm season precipitation. To test the possibility that the four scenarios were not randomly distributed, which might influence results by defining temporally and climatically distinct periods, we conducted Kruskal-Wallis tests on the years in which the four scenarios (LW, LD, SW, SD) occurred. Over 96% of pixels (at the 1% level) showed no differences: we assumed no bias in the timing of the scenarios and assessed the seasonal and annual NEE patterns associated with each category.

Field observations

We obtained 1992–2001 daily NEE values from the Harvard Forest eddy-covariance site (42.5357°N, 72.1719°W, <http://www-as.harvard.edu/chemistry/hf/>) and processed the data to obtain annual NEE and carbon uptake period. Spring phenology has been rigorously measured at the Harvard Forest with fall measurement on a more intermittent basis (2001 unavailable, <http://lternet.edu/hfr/data/hf003/hf003.html>). We therefore used only spring data and, for the stage at which 50% of buds showed recognizable leaves, calculated mean dates for three categories: (1) all species, (2) dominant species only (*Quercus rubra*, *Quercus alba*, *Quercus velutina*, *Tsuga canadensis*, *Betula lenta*, and *Acer rubrum*), and (3) *Quercus rubra*, the species with the highest coverage. We then related carbon uptake period and these leaf phenology metrics to annual NEE. Due to the short time record, we did not divide the dataset into the LW, LD, SW, and SD categories.

Results

Simulation results for the DBF indicated that in general, physical phenology as measured by canopy duration was strikingly unrelated to annual NEE (Fig. 1 and Table 1). For the canopy duration vs NEE relationship, the mean R^2 was 0.032 with a slope of $2.7 \text{ g C m}^{-2} \text{ yr}^{-1}$ per one day increase in canopy duration (Table 1). Only 21% of the 1167 pixels had a significant relationship at the 1% level. Mann-Whitney U -tests for differences in NEE between years with longer than average canopy duration and shorter than average canopy duration also showed that only 16% of pixels had significant differences at the 1% level. We therefore were unable generally to reject the null hypothesis of no relationship between canopy duration and NEE. Conversely, carbon uptake period was highly related to NEE (Fig. 1) with a mean R^2 of 0.66 and a slope indicating an increase of $5.4 \text{ g C m}^{-2} \text{ yr}^{-1}$ per one day increase in carbon uptake period (Table 1). All pixels had a statistically significant regression leading us to reject the null hypothesis of no relationship between carbon uptake period and NEE. For both the

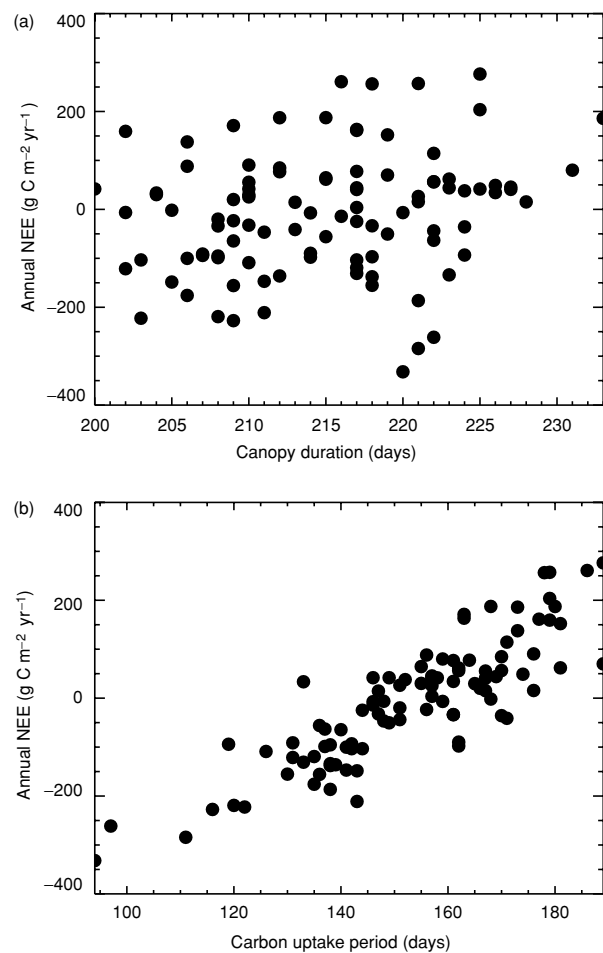


Fig. 1 Scatter plots for a representative 1895–1993 simulation of (a) canopy duration vs NEE and (b) carbon uptake period vs NEE.

Table 1 Mean relationships between phenological metrics and annual net ecosystem exchange (NEE) for 1167 eastern United States deciduous broad leaf forest pixels (1895–1993 simulations)

	Canopy duration vs NEE	Carbon uptake period vs NEE
R^2	0.032	0.66
Slope	2.7	5.4
% sig.	21	100

Canopy duration is the number of days from leaf appearance to complete leaf fall. Carbon uptake period is the number of days with net uptake of carbon. Statistics are: R^2 , the coefficient of determination; slope, the slope of the relationship ($\text{g C m}^{-2} \text{ yr}^{-1}$ /change in explanatory variable); and percentage sig., the percent of the 1167 pixels showing a relationship significant at the 1% level.

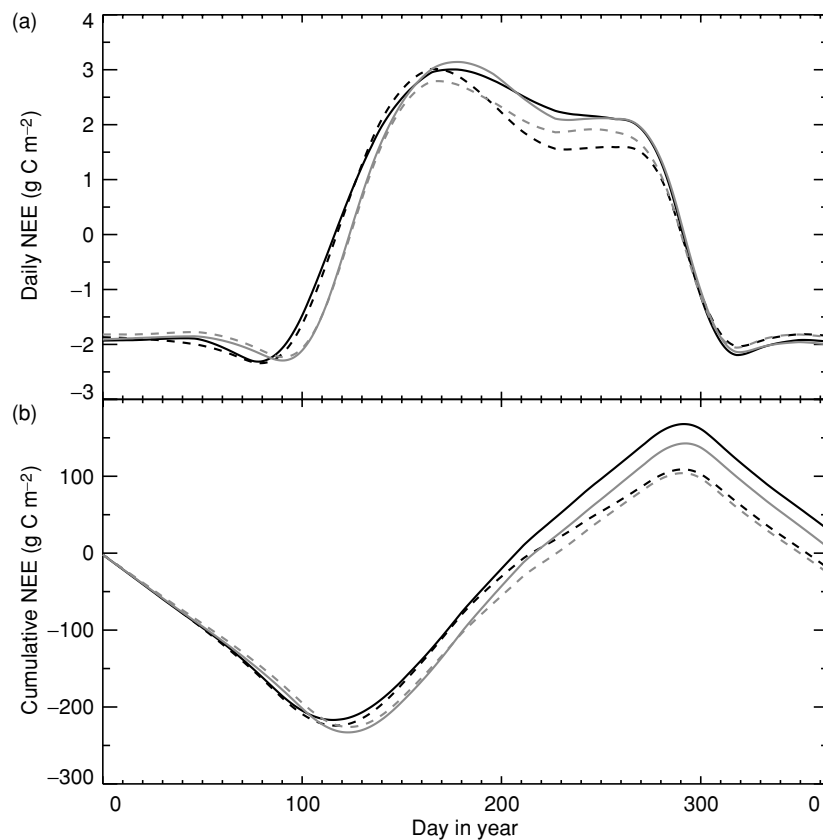


Fig. 2 Daily NEE in the four canopy duration/warm season precipitation scenarios. Scenarios are LW (solid black line), LD (dashed black line), SW (grey solid line), and SD (dashed grey line). Where L = longer than average canopy duration. S = shorter than average canopy duration. W = wetter than average warm season precipitation. D = drier than average warm season precipitation. Curves are the average of 1167 pixels, smoothed with a 30-day window. Sign convention: negative = net carbon release; positive = net carbon uptake. (a) Daily values of NEE for the four scenarios (b) Annual accumulation of daily NEE values. The influence of precipitation can be seen by comparing the LW and LD scenarios while temperature effects (as manifested in canopy duration) are apparent between the LW and SW scenarios.

relationships shown in Table 1, correlations were highest in the current year, suggesting that the effects of phenological variation on NEE were not lagged.

Data from the Harvard Forest eddy-covariance site support our simulations. For the mean date at which 50% of buds showed recognizable leaf growth, no significant relationships were found for regressions with all species ($P=0.51$), all dominant species ($P=0.69$), or *Quercus rubra* ($P=0.66$) alone. The carbon uptake period vs NEE relationship at the Harvard Forest was nearly significant at the 5% level ($P=0.059$) and had a slope of $5.2 \text{ g C m}^{-2} \text{ yr}^{-1}$ per one day increase in carbon uptake period, very similar to the 5.4 slope reported for the simulation data (Table 1).

Figure 2, which shows the mean response of the 1167 pixels for the four canopy duration/warm season precipitation scenarios, indicates that precipitation interacted with canopy duration variability. Due to earlier leaf appearance, as shown by the earlier upward trend in daily NEE, the LW and LD scenarios began growth earlier than the SW and SD scenarios. Until approximately day in year 180, the LW and LD curves were quite similar but diverged from day in year 200 to 280. The midsummer drought in the LD case caused a reduction in both net primary production ($\text{NPP} = \text{GPP} - \text{Ra}$)

and Rh. If equal in magnitude, the two effects would have cancelled each other; in reality, the reduction in NPP was about double the reduction in Rh, leading to a nearly three-month reduction in NEE. The short canopy duration scenarios exhibited a delay in the upward trend of the NEE curve (Fig. 2a) caused by a later initiation of growth. The SD scenario followed the SW scenario until again the midsummer drought conditions caused a reduction in NEE. Consequently, with the exception of the spring lag induced by phenological differences, the LW and SW scenarios were similar.

Figure 2(b) shows cumulative NEE curves for the four scenarios. In order from highest to lowest NEE, they were LW, SW, LD, SD. Divergence based on precipitation levels initiated at about day in year 180 for both long and short canopy duration conditions. Until yearday 100, the short canopy duration scenarios had higher (less negative) NEE due to reduced Rh caused by cooler winter and spring temperatures.

Kruskal-Wallis tests of differences among the LW, LD, SW, and SD scenarios showed that of the 1167 pixels, the percentage of significant differences was 68% at the 1% level and 82% at the 5% level. In 84% of pixels, the LW scenario produced the highest average NEE followed by the SW (9.9%), LD (5.6%), and SD (<1%).

Discussion

Two broad conclusions may be drawn from the simulation results shown here. First, the ecophysiological growing season, as defined by the carbon uptake period, is a strikingly good predictor of annual NEE. That the total number of days with net carbon uptake is a good predictor of the annual total is perhaps an unsurprising result. Nonetheless, the results shown here are in general agreement with results from the Harvard Forest eddy-covariance site and separate systematic eddy-covariance analyses and suggest that a remote sensing approach to monitor carbon uptake period would be extremely valuable (Schimel, 2001).

Second, the physical growing season alone, as defined by canopy duration, is not a good predictor of annual NEE. Findings by (Barber *et al.*, 2000) that drought conditions can negate the effects of warmer temperatures are consistent with our finding that LD scenarios usually had lower NEE than SW years (Fig. 2). Starr *et al.* (2000) found a similar lack of responsiveness to the timing of plant growth in arctic plants. These results are not in conflict with White *et al.* (1999a), in which simulations using a dynamic canopy duration model were compared to simulations using static canopy duration (i.e. plants began and ended growth on the same day every year). White *et al.* (1999a) showed that, for example, if static phenology was used when in reality the canopy should have appeared one week earlier, NEE would have been underestimated by approximately 11%. They did not, as we have here, specifically address the impact of inter-annual variability in canopy duration alone.

Estimates of earlier growth (Myneni *et al.*, 1997; Zhou *et al.*, 2001) combined with global climatological studies indicating a trend toward increased precipitation (Dai *et al.*, 1997) suggest that in the late twentieth century, at least some regions may have experienced conditions similar to our long canopy duration and high warm season precipitation scenario. We speculate that future changes in the amount or timing of precipitation could alter the apparent association of longer canopy duration with increased carbon storage. Our simulations, as they represent quasi-equilibrium conditions, may miss unique relationships between canopy duration and NEE arising from site disturbance history, stand age, or anthropogenic influences. Fundamentally different relationships may also exist outside the eastern United States DBF. Nonetheless, our findings argue for a more thorough inclusion of precipitation variation in global carbon studies, which to date have been dominated by temperature analyses.

Finally, these results highlight the potential for confusion in phenological research. The physical and ecophysiological definitions of GSL presented here exhibited

vastly different relationships with NEE. At the Harvard Forest, 'Inter-annual variations (in NEE) reflect effects of weather and climate on ecosystem characteristics such as ... length of the growing season ...' (Barford *et al.*, 2001) which could be interpreted to mean canopy duration affects NEE. In fact, the authors were referring to carbon uptake period (S. Wofsy, pers. comm.). Demonstrable relationships between carbon uptake period and NEE therefore can be, and are, interpreted to mean that canopy duration and other phenological metrics are also good NEE predictors. We submit that this is an inaccurate assumption and argue for the use of specifically defined terminology, such as carbon uptake period or canopy duration, instead of the generic term growing season length.

Acknowledgements

We wish to thank Steve Long, Ranga Myneni, and two anonymous reviewers for helpful suggestions and John O'Keefe for maintaining the Harvard Forest field phenology research. This research was supported by the NASA Earth Science Enterprise, primarily from grant NAG5-11282, and by NSF grant GEO-0222701.

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